Chapter 6

Biodiversity Patterns and Processes on the Mid-Atlantic Ridge

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6.1 Introduction

The network of mid-ocean ridges constitutes the largest continuous topographic feature on Earth, 75,000 km long (Garrison 1993). Some of the known chemosynthetic ecosystems (Chapter 9) in these deep seafloor habitats have been relatively well studied, but remarkably little is known about ridge-associated pelagic and benthic fauna that are sustained by photosynthetic production in association with mid-ocean ridges (Box 6.1). This knowledge gap inspired the initiation of the multinational field project "Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic", MAR-ECO (Bergstad & Godø 2003; Bergstad *et al.* 2008c). Extensive investigations were conducted along the Mid-Atlantic Ridge between Iceland and the Azores (Fig. 6.1) with the aim to "describe and understand the patterns of distribution, abundance, and trophic relationships of the organisms inhabiting the mid-oceanic area of the North Atlantic, and to identify and model ecological processes that cause variability in these patterns". Compared with other mid-ocean ridge sections the Mid-Atlantic Ridge region under consideration is special in that it is shallow and emerges at both ends with islands, namely Iceland and the Azores. There have been fisheries since the

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Box 6.1

Historical Context

In 1910, the R/V *Michael Sars* expedition across the North Atlantic (Murray & Hjort 1912) revealed markedly elevated abundance and species numbers in shallow mid-ocean areas, including approximately 45 fish species and well over 100 invertebrates new to science, many of which came from what later would be recognized as the Mid-Atlantic Ridge (MAR).

The general bathymetry of the North Atlantic mid-ocean ridge was mapped by the early 1960s and studies of oceanic circulation across the ridge and deep water flow through the Charlie Gibbs Fracture Zone (CGFZ) were well advanced by the start of MAR-ECO field work (see, for example, Krauss 1986; Rossby 1999; Bower *et al.* 2002). Gradually improved bathymetric data revealed the axial valley, numerous hills and valleys, and major fracture zones reaching abyssal depths. Circulation features are shown in Figure 6.1, including the Sub-Polar Front (SPF), which crosses the ridge in the vicinity of the CGFZ at around 52° N and may be significant to biogeography.

The SPF separates the Cold Temperate Waters Province (CTWP), and the Warm Temperate Waters Province (WTWP), defined by The Oslo–Paris Commission (OSPAR) based on extensive reviews of the regional biogeography data (Dinter 2001). Provinces defined by Longhurst (1998) were mainly based on surface features, one of them being an east–west asymmetry in the diversity patterns of zooplankton in the central North Atlantic (Beaugrand *et al.* 2000, 2002). Biogeography of the bathyal benthic fauna at the northern MAR was addressed in recent studies of the Reykjanes Ridge and seamounts south of the Azores (Mironov *et al.* 2006), but almost no data were available from the CGFZ-to-Azores section of the MAR. On the ocean-basin scale, Mironov (1994) proposed the concept of "meridional asymmetry": specifically, that some western Atlantic species are widely distributed in the Azorean-Madeiran waters whereas the eastern Atlantic benthic invertebrates are confined (with very rare exceptions) to the East Atlantic.

Pelagic and demersal nekton of the northern MAR were investigated by various historical expeditions that crossed the North Atlantic (see, for example, Murray & Hjort 1912; Schmidt 1931; Tåning 1944), and later by the Atlantic Zoogeography Program (Backus *et al.* 1977), and German expeditions to the mid-ocean and seamounts (see, for example, Post 1987; Fock *et al.* 2004). Information existed on the distribution of cephalopods at various specific locations in the Atlantic (Vecchione *et al.* 2010), revealing general latitudinal patterns and information from isolated seamounts, but none were focused on the MAR. Although the fish fauna and general distribution patterns of deepwater fishes of the northern Atlantic Ocean had been described (see, for example, Whitehead *et al.* 1986; Haedrich & Merrett 1988; Merrett & Haedrich 1997), surprisingly few previous studies have focused specifically on the role of the mid-oceanic ridges in the distribution and ecology of either pelagic or demersal fishes. Studies from the Azores have shown very low endemism, and that most species have distributional affinities with the eastern Atlantic and the Mediterranean (Santos *et al.* 1997; Menezes *et al.* 2006). Considerable knowledge of fishes associated with ridge systems has been gained from fisheries-related research (Bergstad *et al.* 2008b, c), but most reports focused strongly on target species and usually on only the shallower parts of the ridge and specific seamounts. Only in exceptional cases have full species lists of the catches been published (see, for example, Hareide & Garnes 2001; Kukuev 2004). Areas of the northern MAR have been, and still are, exploited for fish species such as redfish (*Sebastes* spp.) (Clark *et al.* 2007). Pelagic fisheries of the open ocean have targeted tuna, swordfish, and sharks that tend to be found near fronts, eddies, and islands. Whales also occur in such areas (Sigurjónsson *et al.* 1991) and, like the epipelagic fishes, they migrate extensively, perhaps associated with the MAR.

Life-history strategies had not been studied for any species on the MAR, but information was available for some species on adjacent seamounts or continental slopes. These data constituted valuable comparative sources for new studies of the diversity of life-history strategies characterizing ridge-associated species.

Knowledge of large-scale distributions across and along the MAR was lacking for most pelagic and demersal macro- and megafaunal groups. Basin-wide population connections were also unknown. It was uncertain whether the MAR fauna was unique or composed of elements from the adjacent continental slopes.

MAR food webs were unknown, except for a few studies along the Reykjanes Ridge, and life-history information was only available for a very limited number of zooplankton taxa (copepods, mainly *Calanus* spp.), but lacking for most other species. The general trophic positions of some common zooplankton species, primarily copepods, amphipods, and euphausiids, inhabiting the epi- and upper mesopelagic layers above the Reykjanes Ridge have been described (Magnusson & Magnusson 1995; Petursdottir *et al.* 2008). Also, the spawning aggregations of redfish confined to the western slopes of the Reykjanes Ridge suggest that this is a productive area (Pedchenko & Dolgov 2005). However, no information existed on how the MAR affects productivity or abundance of mesopelagic organisms.

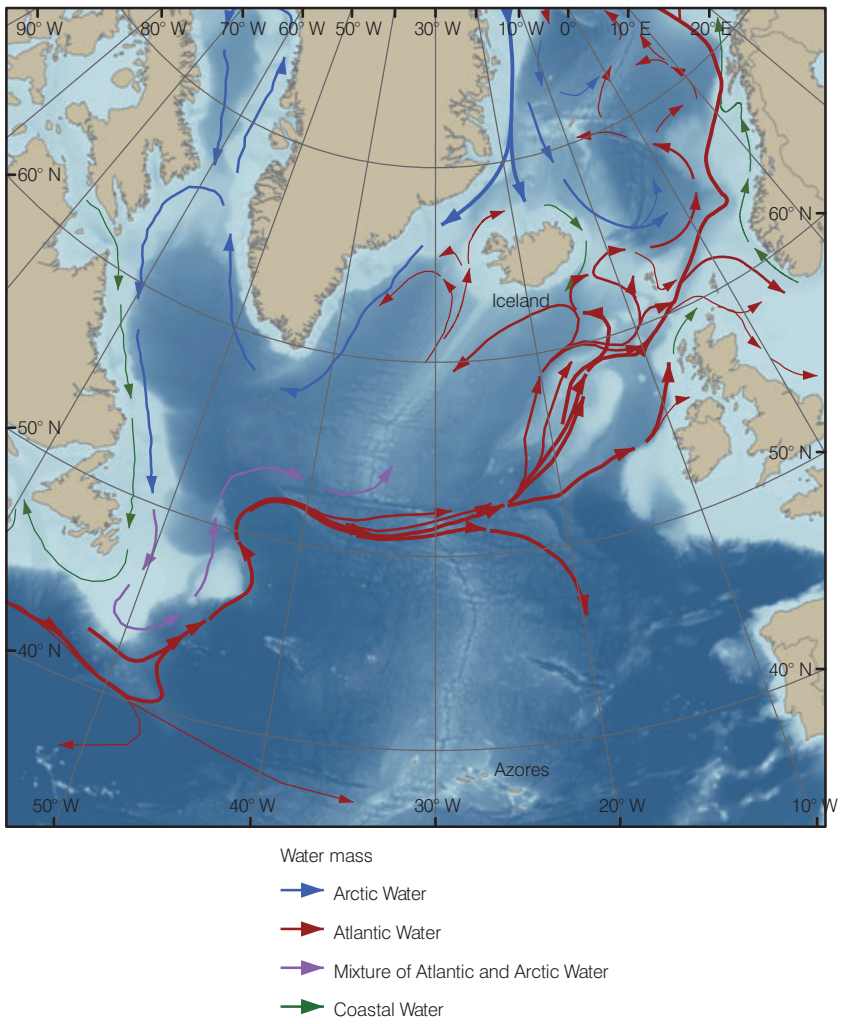

Fig. 6.1
Bathymetry and main circulation features of the North Atlantic.

1970s, and the information available suggested high biodiversity and a strong potential for new discoveries.

6.1.1 The MAR-ECO project

MAR-ECO was conceived as the first comprehensive international exploration of a substantial section of the global mid-ocean ridge system. Working in mid-ocean waters at great depths and in rugged topography is technologically challenging and expensive. MAR-ECO's strategy was to mobilize a cadre of experts, using a variety of instruments and ships from several countries, to achieve the research capacity to meet the many and varied challenges. The "flagship" expedition for this project was conducted by R/V *G.O. Sars* during summer 2004, with concurrent longline fishing by F/V *Loran*, but several other cruises both before and after have contributed substantially as well (www.mar-eco.no). Using multiple technologies on the same platform provides more comprehensive results and enhances the potential for new discoveries. Our goal was to sample and/or observe organisms ranging in size from millimeters to meters (for example small zooplankton to whales), hence many types of sampler were used (Fig. 6.2). To sample all relevant depths, the technologies needed to function from surface waters to at least 3,500 m, preferably as deep as 4,500 m to reach the bottom of the deepest valleys. Along with the sampling of biota, hydrographic data were collected to characterize the physical and chemical environment. In addition to ships, other platforms such as manned and unmanned submersibles, moored instruments, and benthic landers were adopted. These instruments used optics and acoustics, and some were deployed for long periods to collect temporal data for certain taxa or selected features. Detailed accounts of technologies and methods and sampling strategies for the different taxa and functional groups were given by Wenneck *et al.* (2008), Gaard *et al.* (2008), and in many papers describing results of analyses (see, for example, several papers in Gebruk (2008a) and Gordon *et al.* (2008)). Those references also describe methods used in the post-cruise analyses of taxonomy and systematics, trophic ecology, and life-history strategies.

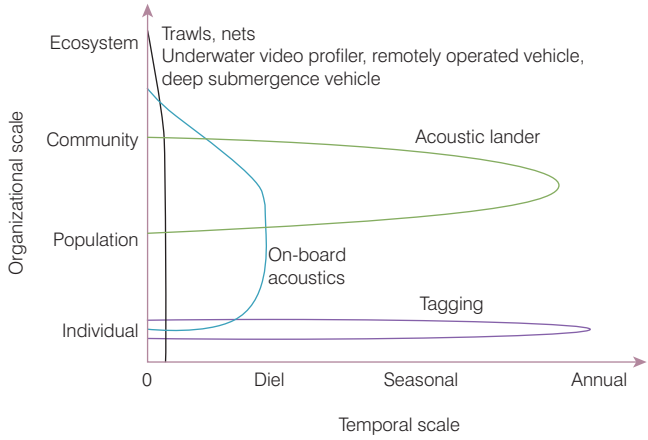

Fig. 6.2
Technologies and their spatiotemporal sampling scales.

6.2 Discoveries

6.2.1 Hydrography

Composite remote-sensing images were prepared to identify the location of the SPF in relation to location of the ridge (Søiland *et al.* 2008). From these and ship-board sampling, four different hydrographic regions were identified in the surface layers. North of 57°N on the Reykjanes Ridge, Modified North Atlantic Water dominated. Between 57°N and the SPF there was Sub Arctic Intermediate Water. South of the SPF, North Atlantic Central Water traverses the ridge in the general eastward flow of the North Atlantic Current but mixing with Sub Arctic Intermediate Water forms in a complex pattern of eddies to south of 50°N. The southern boundary of the SPF was thus very indistinct, containing many features with patches of high productivity and high abundances.

6.2.2 Identification and distribution of the fauna

6.2.2.1 Faunal composition and biodiversity

The number of species recorded in the samples from the two-month 2004 expedition by R/V *G.O. Sars* and F/V *Loran* illustrates the scale of diversity of the MAR-associated pelagic and epibenthic macro- and megafauna comprising animals of sizes from about 1 mm to several meters (Table 6.1). Examples include the 303 species from more than 60,000 fish specimens collected by net sampling during the *G.O. Sars* expedition. Of these fishes, two-thirds or more were pelagic (Sutton *et al.* 2008), the rest demersal (that is, either benthic or benthopelagic (Bergstad *et al.* 2008b)). Many species were extremely rare and some were undescribed (see, for example, Orlov *et al.* 2006; Byrkjedal & Orlov 2007; Chernova & Møller 2008). The pelagic fish diversity was highest in the mesopelagic (200–1,000 m), whereas, surprisingly, biomass was highest in the bathypelagic (greater than 1,000 m). Numerically dominant families of pelagic fishes included Gonostomatidae, Melamphaidae, Microstomatidae, Myctophidae, and Sternoptychidae. The family Macrouridae was prominent among the demersal fishes, represented by 17 species (plus one that is probably new to science). *In situ* observations were also acquired: 22 fish taxa were photographed by a baited benthic lander, whereas bottom-dive segments with remotely operated vehicles (ROVs) found at least 36 taxa, including roundnose grenadier, orange roughy, oreos, halosaurs, codlings, and many additional macrourids. The longline catch comprised mainly large predatory fishes (mean weight 2.4 kg), dominated by the families Etmopteridae, Somniosidae, Ophidiidae, Macrouridae, Moridae, and Lotidae. This represented a different faunal composition from that of the demersal trawl catch.

A substantial cephalopod collection from the midwater and bottom trawls comprised 54 species in 29 families (Vecchione *et al.* 2010). The squid *Gonatus steenstrupi* was the most abundant cephalopod in the samples, followed by the squids *Mastigoteuthis agassizii* and *Teuthowenia megalops*. A multispecies aggregation of large cirrate octopods dominated the demersal cephalopods.

About 10% of species in the MAR-ECO epibenthic invertebrate species appeared to be new to science. The species richness of corals was high with a total of 40 taxa recorded. Octocorals dominated this coral fauna, with 27 taxa. *Lophelia pertusa* was one of the most frequently observed corals, present on five of the eight ROV-inspected sites. Massive live reef structures were not observed; only small colonies (less than 0.5 m across) were present. The number of megafaunal taxa was 1.6 times higher in areas where corals were present compared with areas without corals. Typical taxa that co-occurred with *Lophelia* were crinoids, sponges, the bivalve *Acesta excavata*, and squat lobsters.

Corresponding numbers for zooplankton taxa and top predators such as mammals and seabirds (from sightings along the ship's track) are given in Table 6.1. For all taxa, occurrence data were reported to the Ocean Biogeographic Information System (OBIS) as soon as identifications were validated.

6.2.2.2 Population structure

Many deepwater species have basin-wide distributions, and understanding potential sub-structuring is of substantial ecological and evolutionary interest with direct implications for management. Investigating underlying processes through a comparative assessment of species with differing

Table 6.1

Number of species recorded as of mid-2008.

Main taxa	Identified species	Described new species	Comments	New species references
Cetaceans	14			
Seabirds	22			
Fishes	303	2		Byrkjedal & Orlov 2007; Chernova & Møller 2008
Hemichordates	2	(2)	(Not described.) New species observed but not collected	Holland *et al.* 2005
Brachiopods	3			
Mollusks	75	2	Two new species of cephalopod	Vecchione & Young 2006; Young *et al.* 2006
Arthropods	306	2	One new genus	Brandt & Andres 2008; Crosnier & Vereshchaka 2008
Echinoderms	104	9	One new genus and one new family	Dilman 2008; Gebruk 2008; Martynov & Litvinova 2008; Mironov 2008
Annelids	3			
Chaetognaths	16			
Echiurans	2	1	New species of the genus *Jacobia* (Echiura)	Murina 2008
Sipunculids	2			Murina 2008
Ctenophores	3			
Cnidarians	112			
Sponges	35	13	One new genus	Menschenina *et al.* 2007; Tabachnick & Menshenina 2007; Tabachnik & Collins 2008
Fish parasites:				
Nematodes	11	2		Moravec *et al.* 2006; Moravec & Klimpel 2007
Monogeneans	18	1		Kritsky & Klimpel 2007
Cestodes	6			
Acanthocephalans	3			
Crustaceans	8			
Total	1048	34		

life-history characteristics (for example, duration of larval stages, fecundity, longevity, and habitat requirements) allows predictions about expected boundaries to gene flow, rates of gene flow, and demographic history. However, there have been some unexpected results. For example, the orange roughy (*Hoplostethus atlanticus*) has life-history characteristics that could promote population structure (for example, long life, comparatively low fecundity and larval duration), but genetic data suggest no structure in the North Atlantic study area (White *et al.* 2009; S. Stefanni, unpublished observations). On the other hand, the round-nose grenadier (*Coryphaenoides rupestris*), which has characteristics suggesting greater connectivity, showed considerable structure at the ocean-basin scale (H. Knutsen, P.E. Jorde & O.A. Bergstad, unpublished observations), some small-scale structure across a putative boundary (the sub-polar front), and evidence for selection associated with depth (White *et al.* 2010). In general the comparative studies highlight the importance of several key factors (Fig. 6.3): local habitat dependence (for example, tusk (*Brosme brosme*) in the MAR; Knutsen *et al.* 2009), isolation by geographic distance or along current pathways (see, for example, Knutsen *et al.* 2007), oceanic barriers to gene flow (see, for example, White *et al.* 2010), and the role of different life stages (see, for example, White *et al.* 2009).

Demersal fishes in general have low resilience to population disturbance, with a population doubling time on the order of 10 years. The existence of local, autonomous populations implies that local fishing areas may be sensitive to overexploitation. Our findings highlight the importance of considering population structure in deep-sea fishery management.

6.2.2.3 Taxonomy and phylogenetics

Extensive work on phylogenetic reconstruction for species discovery and to determine the origin of MAR radiations is ongoing. DNA barcoding of MAR species is proceeding. Most species of both pelagic and demersal nekton (fishes, cephalopods, and shrimps) will be barcoded. For example, over 190 fish species have been barcoded for the first time from MAR-ECO material. For zooplankton, species barcoding is being coordinated with the Census of Marine Zooplankton project (Chapter 13).

For two morphologically cryptic species (*Aphanopus carbo* and *A. intermedius*) with overlapping distributions (Stefanni & Knutsen 2007), a genetic marker suitable for routine discrimination has been developed (Stefanni *et al.* 2009). The huge collections of specimens and tissue samples including samples of very rare species not available elsewhere, motivated new revisions of difficult taxa. An example is the cusk-eel genus *Spectrunculus*, which was revised and split from one to two species based mainly on MAR-ECO material (Uiblein *et al.* 2008). The samples of rare deep-sea fishes are also very valuable in studies of the evolution of various groups. Modern standards for these phylogenetic reconstructions and studies of the interrelationships and origin of the fauna require tissue samples for DNA sequencing and corresponding voucher specimens for morphological characters and identification. Published studies based on MAR-ECO material include the slickhead and tubesholder fishes (Alepocephaliformes) (Lavoue *et al.* 2008, Poulsen *et al.* 2009), and several others are in progress (Ophidiiformes, Myctophidae).

6.2.3 Vertical distribution

6.2.3.1 Zooplankton

Copepod abundance was highest in upper layers (0–100 m) and decreased exponentially with depth (Gaard *et al.* 2008). Several species of copepods and decapods were observed to deepen their vertical distributions towards the south, following the isotherms (that is, equatorial submergence). Decapods peaked in the 200–700 m stratum north of the SPF, and at 700–2,500 m depth south of the SPF. The highest densities of euphausiids were found in the upper 200 m. The gelatinous fauna, dominated by cnidarians, siphonophores, and appendicularians, was most abundant at 400–900 m (Stemmann *et al.* 2008; Youngbluth *et al.* 2008). *In situ* observations of gelatinous zooplankton revealed that different taxa occurred in distinct, and often narrow (tens of meters), depth layers (Vinogradov 2005; Youngbluth *et al.* 2008). The most important contributors to the cnidarian biomass (wet mass) north of the SPF were the scyphomedusae *Periphylla periphylla* and *Atolla* spp. The vertical distributions of *P. periphylla* and *Atolla* spp. were deeper during the day than at night. The bulk of the *Atolla* spp. population usually resided deeper in the water column than *P. periphylla*. Appendicularians were generally abundant at 450–1,000 m and were observed to accumulate in the lowermost 50 m (Vinogradov 2005; Youngbluth *et al.* 2008), suggesting that these feeding specialists (extremely small particles) are a prominent component of the benthopelagic zooplankton.

6.2.3.2 Pelagic nekton (fishes and cephalopods)

Depth was by far the most important determinant of faunal composition for pelagic fish species, with along-ridge variation secondary. The most surprising finding was the water-column maximum fish biomass between 1,500 and 2,300 m (Sutton *et al.* 2008); this pattern stands in stark contrast to the typical exponential decline in fish biomass below 1,000 m seen in open oceanic ecosystems. Furthermore, evidence from acoustics and trawl catches suggests that in some locations, deep pelagic fish abundance and biomass peak within the benthic boundary layer, suggesting the possibility of predator–prey relationships between demersal fishes and migrating pelagic fishes as a mechanism underlying

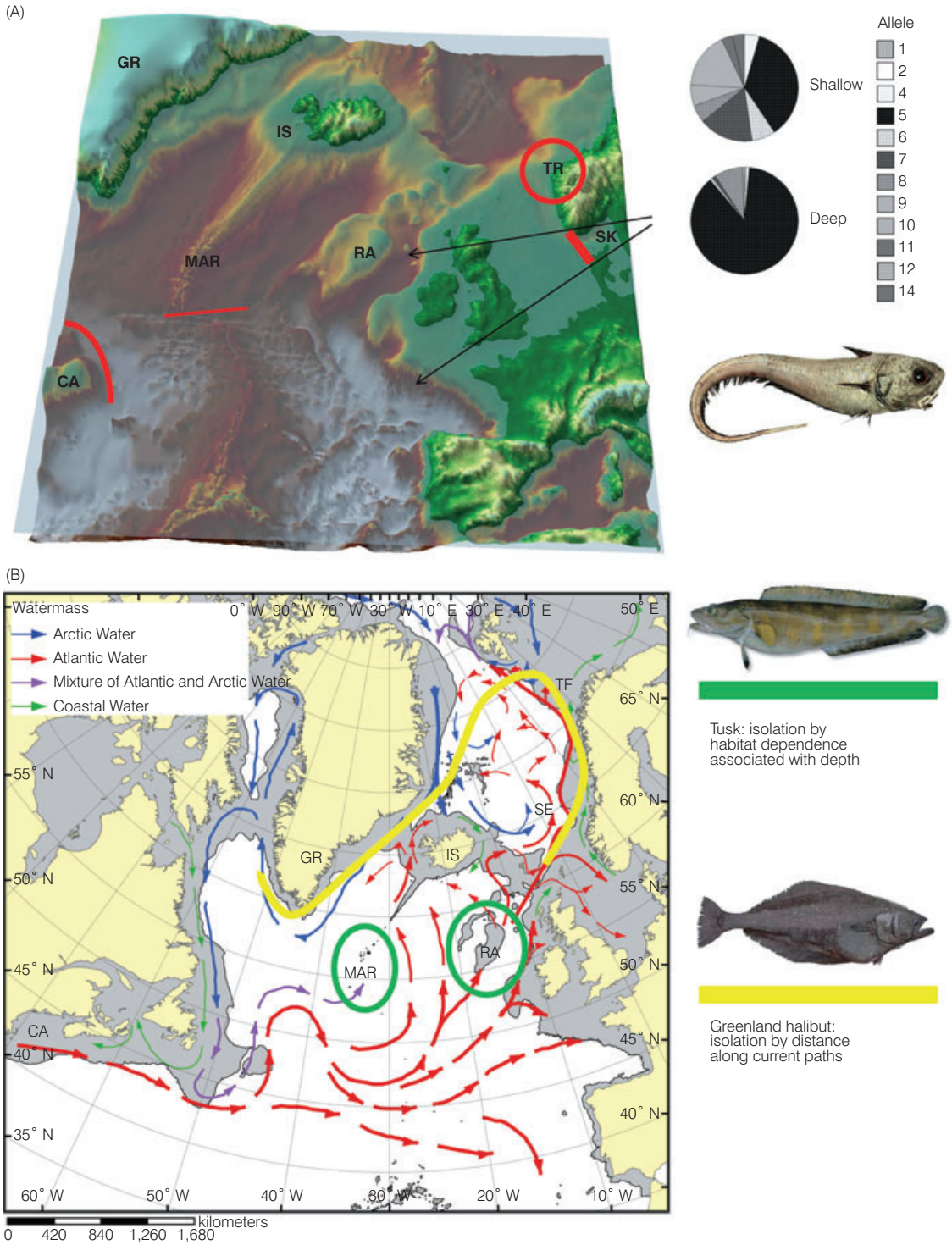

Fig. 6.3

(A) Barriers to gene flow (after H. Knutsen, P.E. Jorde & O.A. Bergstad, upublished observations; White *et al.* 2010) and evidence for local adaptation (after White *et al.* 2010) in *Coryphaenoides rupestris*. Barriers are shown in mid-Atlantic ridge (MAR); RA, Rockall; TR, Trondheim coastal site; SK, Skagerrak; IS, Iceland; GR, Greenland; CA, Canada. The allele frequency pie charts show how allele 5 (at a microsatellite DNA locus evidently linked to a relevant functional gene) is associated with depth of sample. MAR = 2,563–2,573. **(B)** Illustration of isolation by distance along current paths for Greenland halibut (yellow), and local differentiation of *Brosme brosme* populations (likely associated with depth) (green). SE, Storegga; TF, Tromsøflaket.

enhanced demersal fish biomass over the MAR (Bergstad *et al.* 2008b).

Acoustic data from both vessel and stationary systems revealed biophysical interaction of presumed importance to production and species interactions. In the epi- and mesopelagic zones (0–1,000 m) of most areas along the MAR a clear diel vertically migrating community was observed by acoustics, with daytime depths of 500–1,000 m, and nighttime occupation of surface layers (Opdal *et al.* 2008). The range and the patterns were affected by topography and light levels that may have been affected by phytoplankton density. Lanternfishes and pearlfishes (Sternoptychidae) were the dominant diel vertically migrating fishes. Seasonal information from an upward-looking acoustic lander showed abrupt changes in distribution and abundance of sound scatterers in early autumn and spring (Doksæter *et al.* 2009). Vertical migration was reduced to a minimum during mid-winter and peaked during summer.

Mesoscale eddies, validated by satellite sea level altimetry data, were recorded from the surface to 1,200 m. The acoustic lander observed extensive internal wave activity, mainly close to the seabed, but sometimes extending into the entire water column from 900 m to the surface. Occasionally, breaking internal waves apparently created turbulence in the near bottom zone resulting in disruption of scattering layers and chaotic distribution of individual acoustic scatterers.

Observations from submersibles have shown some cirrate octopods (*Grimpoteuthis* and *Opisthoteuthis*) to sit on the bottom and/or to float just above it (Vecchione & Roper 1991; Vecchione & Young 1997; Felley *et al.* 2008). All specimens of these genera, as well as *Cirroteuthis* and *Cirrothauma*, were collected in the bottom trawl. Conversely, many *Stauroteuthis syrtensis* were taken in midwater, including a specimen that had to have been at least 1,690 m above the bottom, although most specimens came from the bottom trawl. It therefore appears that this species aggregates near bottom but its distribution also extends far up into the deep water column.

6.2.3.3 Demersal fishes

Overall, demersal fish biomass and abundance declined with depth from the summit of the ridge to the middle rises on either side. Multivariate analyses of catch data from trawls and longlines (Bergstad *et al.* 2008b; Fossen *et al.* 2008) revealed that the species composition primarily changed with depth and that, as with pelagic fishes, variation by latitude was secondary. Species evenness was higher in deep slope and rise areas than on the slopes. Assemblages of species could be defined for different depth zones and sub-areas. *In situ* observations of scavenging fishes attracted to baited landers revealed three main assemblages: shallow (924–1,198 m), intermediate (1,569–2,355 m), and deep (2,869–3,420 m). These assemblages were dominated respectively by three species, *Synaphobranchus kaupii*, *Antimora rostrata*, and *Coryphaenoides armatus*. Abyssal species were found in the axial valley region (*C. armatus*, *Histiobranchus bathybius*, and *Spectrunculus* sp.). Fishing by longlines in rugged terrain at all depths resulted in catches dominated by elasmobranchs (sharks and skates). Fishes were observed during the dives in 2003 of the manned submersibles MIR 1 and 2 in the CGFZ between 1,700 and 4,500 m (Felley *et al.* 2008). Perhaps the most remarkable observation was that of rich densities of small juvenile macrourids in the deep soft-bottom areas, presumably dominated by the abyssal grenadier *C. armatus*. MAR-ECO data formed a significant element of a global analyses of the depth distribution of elasmobranch and teleost fishes, demonstrating that elasmobranchs are uncommon or rare deeper than 3,000 m (Priede *et al.* 2006).

6.2.3.4 Benthos

For a range of taxa from many depths new species were described (Table 6.1). Corals were observed at all MAR-ECO sites inspected with ROVs at bottom depths between 800 and 2,400 m, but were most common shallower than 1,400 m. The deepest record of *Lophelia* was at 1,340 m, south of the CGFZ. Accumulations of coral skeleton debris were observed at several locations, indicating presence of former *Lophelia* reefs.

Manned submersible dives in the CGFZ from 1,700 to 4,500 m observed scattered rich sponge gardens. Dense aggregations of small elpidiid holothurians, *Kolga* sp., occurred at abyssal depths (4,500 m) in a sediment-filled depression. Abundance/biomass of giant protists (foraminiferan Syringamminidae, reaching the size of a golf ball) was noteworthy north of the SPF.

6.2.4 Variation along the ridge

The number of species recorded showed a clear latitudinal pattern for most taxa, with a discontinuity at about the location of the SPF (Fig. 6.4).

6.2.4.1 Zooplankton

The assemblages of copepods, cnidarians, chaetognaths, gelatinous zooplankton, and macrozooplankton were related to the distribution of three main water masses in the area (Gaard *et al.* 2008; Hosia *et al.* 2008; Pierrot-Bults 2008; Stemmann *et al.* 2008): a northern assemblage in Modified North Atlantic Water, a southern assemblage in North Atlantic Central Water, and a frontal assemblage influenced by North Atlantic Central Water and Sub-Arctic Intermediate Water. The species richness of most taxa was found to increase towards the south (Copepoda, Cnidaria, Decapoda, Euphausiacea, Amphipoda, Chaetognatha). Temperature appeared to be the most important factor in determining the structure of the copepod communities.

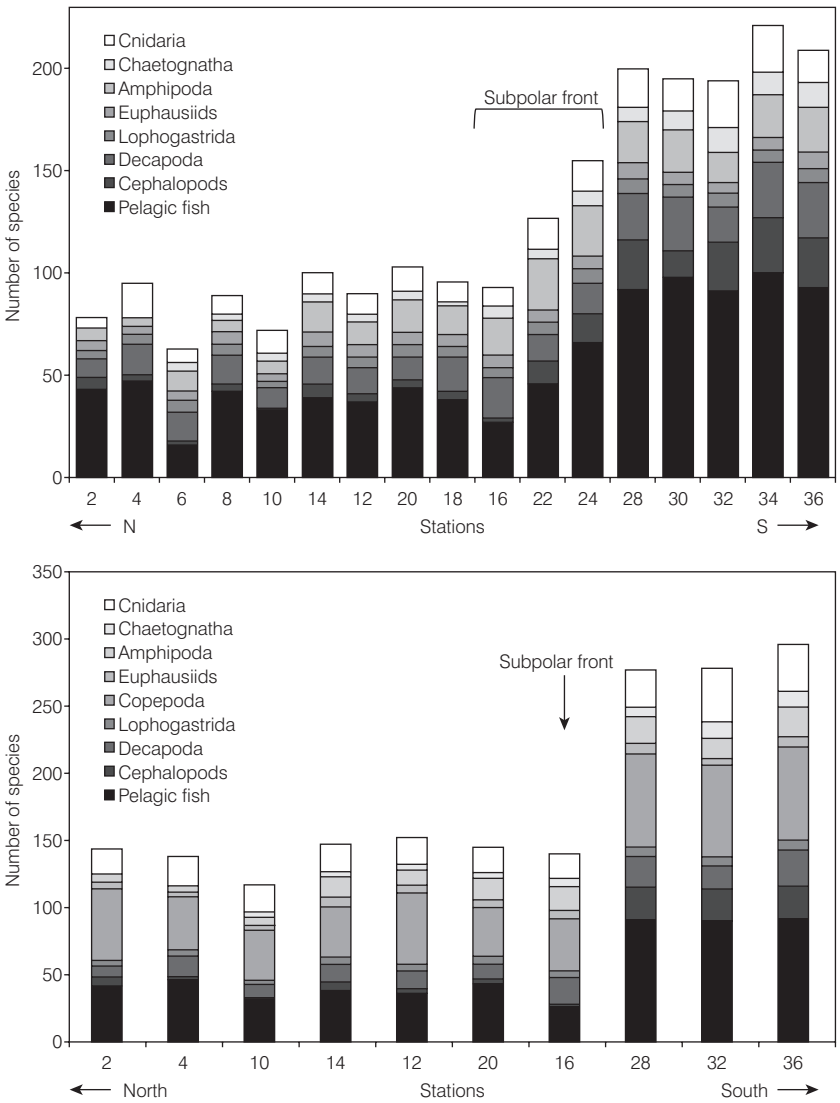

Fig. 6.4
Occurrence of species of various higher taxa at different stations from north (left) to south along the MAR. Top, midwater trawl stations; bottom, mesozooplankton stations.

6.2.4.2 Pelagic nekton

Among cephalopods, the squids *Mastigoteuthis agassizii* and *Teuthowenia megalops* were distributed throughout the whole area; *Gonatus steenstrupi* was most abundant in the northern and central regions (Reykjanes Ridge and CGFZ) (Vecchione *et al.* 2010). In contrast, the bobtail squid *Heteroteuthis dispar* was only common in the Azorean area, with a few specimens near the Faraday Seamounts and the CGFZ. Multivariate analysis revealed a clear separation of a southern cephalopod assemblage (Azorean area), an assemblage confined to the Reykjanes Ridge, and an assemblage concentrated at stations at the CGFZ. The Azorean assemblage was very similar to an assemblage recently described from samples along the Biscay–Azores Ridge and MAR north of the Azores (C. Warneke-Cremer, unpublished observations). Cephalopod species richness per station clearly increased from north to south (five species at a station on the Reykjanes Ridge, 28 species at a station near the Azores). Several benthic and one pelagic species, all taken in small numbers, were captured only in the CGFZ. Numbers of common benthopelagic species were highest in the CGFZ (Vecchione *et al.* 2010).

Within the top 750 m of the water column, there were two primary faunal groups of pelagic fishes (Sutton *et al.* 2008): a higher abundance, lower diversity assemblage from Iceland to the Faraday Seamount Zone (numerically dominated by the lanternfish *Benthosema glaciale*), and a lower abundance, higher diversity assemblage in the region of the Azores (29 lanternfish species contributed half of total abundance). Below 750 m there was a large assemblage of deep meso- to bathypelagic fishes that spanned from the Reykjanes Ridge all the way to the Azores (numerically dominated by the bristlemouth, *Cyclothone microdon*).

6.2.4.3 Demersal nekton

The latitudinal variation in occurrence of demersal fishes caught in demersal trawls was greater in shallow than in deep areas. The number of species was inversely related to latitude, but declined with depth below the slope depths. For example, the macrourids *Coryphaenoides rupestris*, *C. brevibarbis*, and *C. armatus* rank among the most abundant demersal fishes on the ridge or in the deep axial valleys or fracture zones, while other members of the family are uncommon or rare (Bergstad *et al.* 2008a). Whereas a few species in the family apparently have restricted northerly or southerly distributions, most are widespread, but showing definite depth-related patterns of distribution (Fig. 6.5). Similar patterns were observed in the demersal predators sampled by longlines.

6.2.4.4 The Sub-Polar Front: a biogeographic barrier

The SPF acted as a boundary for several zooplankton taxa (Falkenhaug *et al.* 2007). For copepods this delineation was asymmetrical: sub-tropical and warm-temperate species had limited dispersal northward, whereas cold-water species often extended south of the SPF (Gaard *et al.* 2008). The spatial distribution of the dominant copepods, *Calanus finmarchicus* and *C. helgolandicus*, was separated at the SPF, with the latter found only south of the SPF, at depths associated with Mediterranean water masses. The separation of Cnidaria at the SPF was found to be strongest in the upper 500 m but apparent down to 1,500 m (Hosia *et al.* 2008). Epi- and mesopelagic fish distributional trends mirrored those of zooplankton, with species diversity substantially higher near the Azores, but again with cold-water forms common in the south of the SPF (that is, a "fuzzy" southern limit to distribution of northern species). Overall, the strength of the SPF as a boundary to pelagic fauna varied vertically, with deeper-water samples showing less variation in species composition. For epibenthic fauna, changes were observed between the CGFZ and the Azores, particularly in the region of the SPF. The abundance of benthos is higher north of the SPF.

6.2.4.5 A site of enhanced biota

Chlorophyll *a* (Chl *a*) concentrations were elevated in the SPF/CGFZ area (approximately 50–100 mg Chl *a* m^{-2}, 0–30 m) compared with other regions along the ridge (approximately 10–50 mg Chl *a* m^{-2}, 0–30 m) (Gaard *et al.* 2008; Gislason *et al.* 2008; Opdal *et al.* 2008). Several zooplankton taxa were more abundant in the SPF region than elsewhere, for example *Calanus* (Gislason *et al.* 2008), *Pareuchaeta* (Falkenhaug *et al.* 2007), Decapoda (unpublished data), Chaetognatha (Pierrot-Bults 2008), and gelatinous megaplankton (Youngbluth *et al.* 2008). Interestingly, most these taxa are predatory. The area of elevated Chl *a* at the SPF corresponded with an area of elevated rates of egg production by *Calanus finmarchicus* (Gislason *et al.* 2008). Elevated bioluminescence at the SPF (Heger *et al.* 2008) also coincided with higher zooplankton abundances

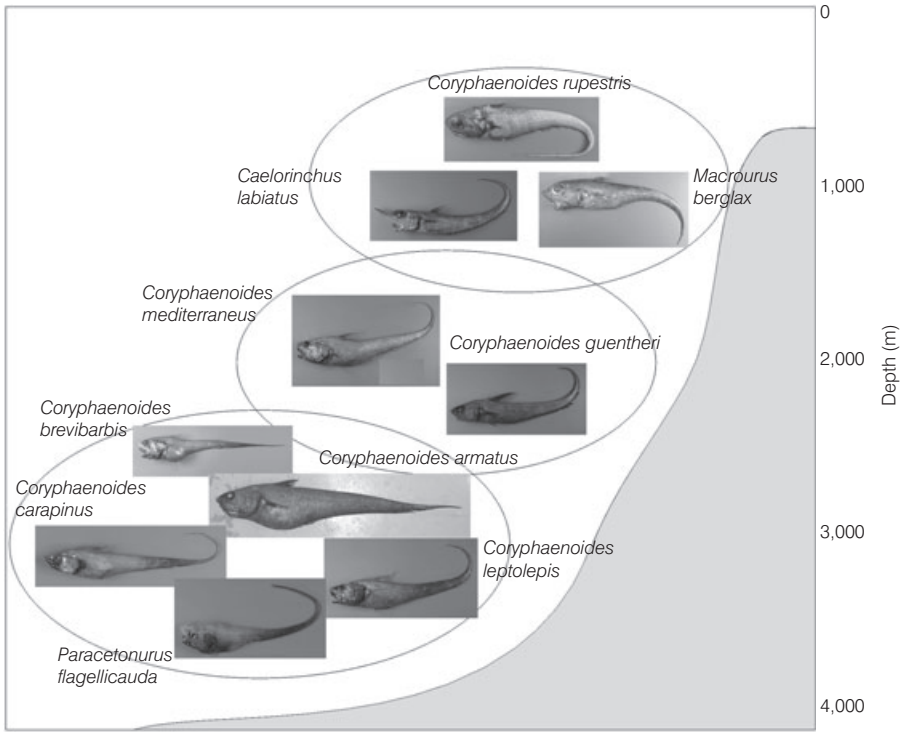

Fig. 6.5
Depth distribution of macrourid fishes from the summit of the MAR to the lower slopes. Adapted from Bergstad *et al.* (2008a).

in this region. The most likely producers of the bioluminescence are crustaceans (decapods/euphausiids) and gelatinous zooplankton. In contrast, lower abundances in the total copepods were recorded in the CGFZ (Gaard *et al.* 2008).

The density of sound scatterers, presumably dominated by fishes, was highest in the CGFZ area and in association with the SPF. In this area, higher densities tended to be associated with marked topographical features, that is, hills or troughs. There appeared to be a positive relation between horizontal distribution of standing stock of phytoplankton as measured by Chl *a* and acoustic backscattering. High abundances of demersal fishes were also found in the SPF (King *et al.* 2006; Bergstad *et al.* 2008b; Fossen *et al.* 2008).

Observations on seabirds and cetaceans unambiguously point to the surface manifestation of the SPF near the CGFZ as the most important large-scale habitat feature for several species of planktivores as well as nekton feeders along the MAR. Results indicate general co-occurrence between these top predators and concentrations of potential prey like squid, pelagic fishes, and macrozooplankton in the CGFZ. Synoptic acoustic and visual transects across the ridge and individual seamounts indicated a segregation of sei whale (*Balaenoptera borealis*) and sperm whale (*Physeter macrocephalus*) in relation to topography. Multivariate analyses of the distribution of the two species with concurrent water current measurements (from acoustic Doppler current profilers) and hydrographic and topographic data at various spatial scales indicated that small-scale frontal processes interacting with the topography in the surface and subsurface waters just north of the surface SPF are important for the transfer of energy to higher trophic levels in the MAR.

6.2.5 Cross-ridge (east–west) patterns of distribution

Cross-ridge patterns of zooplankton were less clear than along the ridge. Data on distributions of copepods and amphipods showed indications of east–west differences in species composition. More warm-water species (for example *C. helgolandicus*) were found east of the ridge (Gaard *et al.* 2008) than to the west. The northeastward trajectory of the North Atlantic Current may enable species of the warm-temperate association to be present east of the MAR and north to 50°N. As a result, the northern distribution limit of warm-water species is farther north on the eastern side than on the western side of the ridge.

Cross-ridge differences in pelagic fish distributions were not detectable by multivariate analysis of catch data (Sutton *et al.* 2008). Similarly, cross-ridge differences in demersal fish distributions were apparently minor, but pairwise comparisons of trawl stations at the same depth and latitude on either side of the central rift valley indicate that such differences may occur.

6.2.6 Food webs and carbon fluxes

Estimated phytoplankton ingestion rates by copepods were not higher at the SPF/CGFZ than in the other areas, indicating that the relatively high production of copepod eggs in the CGFZ is mainly fueled by sources of energy other than phytoplankton (for example microzooplankton) (Gislason *et al.* 2008). *Calanus* spp. are very important in the pelagic ecosystem over the northern MAR as food for organisms at higher trophic levels. Two main trophic pathways were inferred over the Reykjanes Ridge. In one, *Calanus* spp. are important in the diet of *Maurolicus muelleri*, *B. glaciale*, and *Sergestes arcticus*, whereas in the other pathway *Meganyctiphanes norvegica* is the dominant food for the redfish *Sebastes mentella* and *Calanus* are of less importance (Petursdottir *et al.* 2008). For *S. arcticus*, *Calanus hyperboreus* is an important part of the food. Additionally, *S. arcticus* probably has a benthic component in the diet (Petursdottir *et al.* 2008).

Two different types of food web appear to be important on the MAR (Fig. 6.6). One is a classic predatory trophic enrichment with higher levels feeding on those lower. Preliminary analysis of stable-isotopes in the pelagic food web show consumption/conversion of energy from shallow to deep, with a concomitant increase in trophic level: epipelagic fauna to vertically migrating mesopelagic fauna to non-migrating bathypelagic fauna to demersal fauna (trophic levels 2–6). The other, the benthic web, has organisms all essentially feeding on detritus in the sediment but elevated 'trophic' levels (as indicated by δN isotopic values) result from repackaging and remineralization of that material as it passes through the digestive tracts of other deposit feeders. Hence sub-surface feeders have greater δN values than surface feeders.

6.2.7 Life-history studies

The preponderance near the ridge of large, adult bathypelagic fishes (Sutton *et al.* 2008; M. Heino *et al.*, unpublished observations), many in gravid condition (A. Stene, unpublished observations), suggests that the MAR, and perhaps other mid-ocean ridge systems, may be important spawning locations for otherwise widely (basin-wide) distributed fish species. Abundance and distributional data from the MAR-ECO project further suggest that mid-ocean ridges may serve to concentrate deep-pelagic fishes, thereby enhancing reproductive and trophic interactions.

The shapes of length distributions of many common pelagic fish species are unusual, peaking near the maximum known size and with fewer small individuals than normally

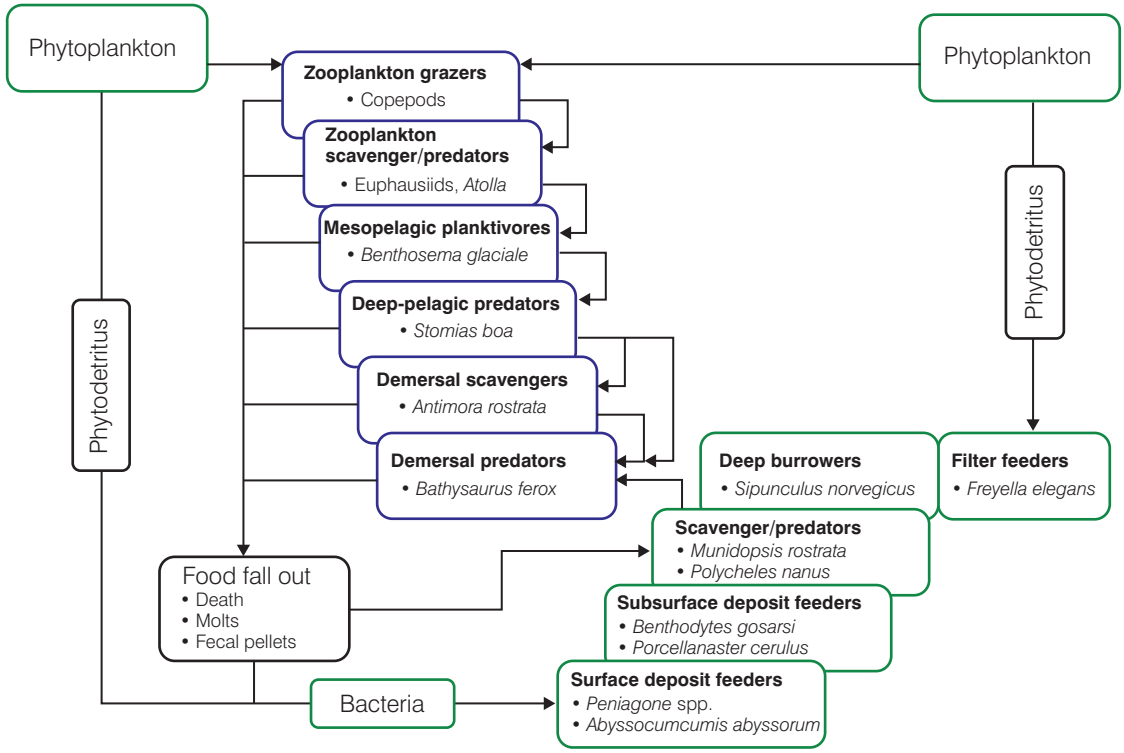

Fig. 6.6

A simplified MAR food web, showing consumption/conversion of energy from shallow to deep, with a concomitant increase in trophic level: epipelagic fauna to vertically migrating mesopelagic fauna to non-migrating bathypelagic fauna to demersal fauna (trophic levels 2–6). Example organisms are given for each trophic step. the benthic "chain" has organisms all feeding on essentially detritus in the sediment but the elevated "trophic" levels (as indicated by δN isotopic values) are a result of repackaging and remineralization of that material as it passes through the digestive tracts of other deposit feeders.

expected – opposite to 'typical' fish length distribution where most individuals are small or intermediate in size. If samples from the MAR resemble the overall population structure (that is, the MAR assemblages do not "overrepresent" adult fishes), then these unusual length distributions suggest that these species have fast growth rate relative to mortality rate. This does not imply that their growth is fast in absolute terms, only that growth outpaces mortality, leading to accumulation of individuals in size classes near the species' asymptotic size.

Small bobtail squids of the species *H. dispar* are the most pelagic members in the family Sepiolidae. During the 2004 *Sars* cruise, 46 specimens were collected in the southern region of the study area (Vecchione *et al.* 2010). All females, including immature specimens, were carrying sperm packages, indicating that the animals can take advantage of chance encounters between the sexes at any time (Hoving *et al.* 2008). Although all female cephalopods can carry or store sperm, the anatomy of the female reproductive system of *H. dispar* suggests that they also fertilize their eggs internally, a reproductive strategy so far unknown for squid or cuttlefish. This reproductive trait, and the small egg size, indicates an adaptation to an oceanic lifestyle, unique within the bobtail squids.

New life-history information was collected for selected demersal fishes. Orange roughy (*Hoplostethus atlanticus*) were not prominent in the MAR-ECO samples, but the few specimens collected comprised very young juveniles of ages 1–2 years and adults within the age range 78–139 years (Tyssebotn 2008). Previous studies have also shown the extended life cycle of this commercially important species, but small juveniles are rarely sampled. A more widespread slope species most abundant at 1,000–3,000 m was the blue hake, *Antimora rostrata*. This species was sampled from the Azores to Greenland (Fossen & Bergstad 2006). *A. rostrata* has intermediate longevity compared with other co-occurring deep-water fishes that have been studied sufficiently. It is neither short-lived, nor especially long-lived. Small juveniles are found in upper slope waters off Greenland, but were rare on the MAR. Hitherto unknown to science, postlarvae of this common species were found on the MAR, indicating that spawning does take place on the ridge (P.R. Møller, unpublished observations).

6.2.8 Management implications

MAR-ECO research has already had conservation implications. Based largely on the results of the *Sars* expedition,

the North-East Atlantic Fisheries Commission (NEAFC) adopted measures that close more than 330,000 km^2 to bottom fisheries on the Mid-Atlantic Ridge, including the area of the CGFZ and SPF (Probert *et al.* 2007) "to protect Vulnerable Marine Ecosystems in the High Seas".

6.3 Knowledge Gaps

The primary remaining gap in current knowledge is the determination of temporal (diel, seasonal, and interannual) variation in faunal composition, abundance, and ecology. The species composition and distribution patterns now described are snapshots from summer seasons, namely after the presumed spring peak in epipelagic production. More extensive sampling into adjacent basins would be needed to determine definitively that observed patterns for pelagic biota are ridge-specific. Few samples with the same methods have ever been collected on adjacent continental slopes, islands, and seamounts; hence it is currently only feasible to assess basin-wide trends relative to impact of ridge for a few faunal components (for example demersal fishes, epibenthos, zooplankton, but not pelagic nekton). To what extent conclusions about structuring of communities by depth, water masses, and frontal zones from the North Atlantic MAR are valid for other sections of the mid-ocean ridge system has not yet been determined.

To enhance knowledge of food web and trophic ecology, the feeding, behavior, and physiology of more species need to be studied. Variables for calculating energy budgets and growth rates are unknown (rates of consumption, excretion, respiration, mortality). To estimate the predation impact of fishes on gelatinous prey, commensurate gelatinous and other zooplankton data on same spatial scales as nekton would be required. Information on the significance of microbial processes (microbial loop) is also needed.

The documented information on the significance of the mid-ocean ridge in the life cycles of nekton and zooplankton remains scattered. Although the occurrence of mature size classes of many nekton species suggests that the ridge is a significant reproduction area, studies of reproduction are lacking for most species. Comparative analyses across taxa would be needed to determine the diversity of life-history characteristics such as longevity, fecundity, and growth. For several demersal fish species, present connectivity between ridge and slope conspecifics appears to be limited, but similar studies for pelagic species are lacking.

Production estimates are few, and the relative significance of different physical and biological processes regulating production and transfer of energy horizontally and vertically remains unclear. Near-ridge zooplankton and pelagic nekton distributions in the entire water column appear to be affected by physical forcing. Without knowledge of the near-ridge flow field many of the potential biotic interactions cannot be substantiated.

6.4 Recommendations

6.4.1 Technologies

Many of the technological challenges for the future are common to studies in many habitats, but are especially pronounced in mid-ocean investigations of large volumes and depth ranges and at great distances from land. Although the analysis of abiotic factors can often be performed in near real-time, processing biological samples can take months and even years. This time lag especially applies to taxonomic studies, basic to studies of structure of assemblages and ecosystem processes. New methods to accelerate identification of organisms and processing of samples should be sought. The underwater video profiler used by MAR-ECO is an example of a major step in this direction. ROVs better adapted for pelagic studies have the potential to provide small-scale data at the individual level for many taxa. Despite advances made by ROV and submersible technology, sampling on rough rocky ground remains challenging. New gear also seems necessary to study the organisms of the benthic boundary layers.

To fill the major gap in temporal dynamics, traditional cruise-based sampling should be supplemented more widely with multiple long-term automatic recording devices using optics and acoustics. Enhancing the depth rating of transducers would be needed to extend the depth to which acoustic landers can be deployed. Current moored acoustic instruments have the potential to monitor sound-scattering zooplankton and nekton of all sizes, and their interactions, at several spatial scales (Fig. 6.7). Observation volume has to increase, however, and species identification has to improve, for example through visual observations or recognition of vocalization. Multiple-frequency sounders facilitate categorizing of the acoustic recordings to some degree, but concurrent targeted trawl sampling is needed to substantiate identification and to reveal details. Low-frequency acoustics may sample at subpopulation scales and high frequencies provide details of millimeter scales.

6.4.2 Strategies for continued exploration of the global ridge system

Mid-ocean ridges circle the globe, and to understand biodiversity patterns and ecological processes of this vast habitat a major multi-year and very costly field effort would be required. This effort would involve ships, observatories, and autonomous vehicles, not to mention the dedication and resources of scientists across the globe. Planning efforts should use new knowledge and experiences gained from these recent studies. Some major conclusions from the North Atlantic may provide guidance for strategic decisions on designs of new field efforts. It

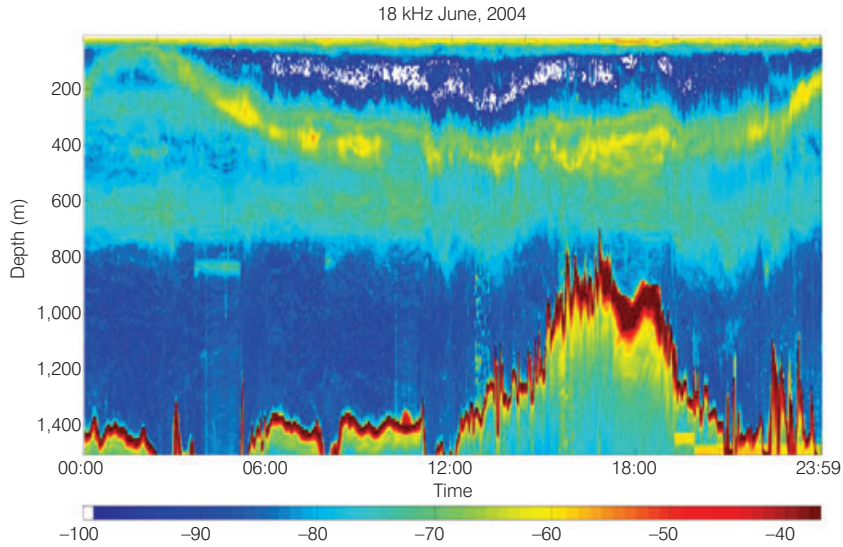

Fig. 6.7

Diel echogram from June 11, 2004, during crossing of MAR (time axis is in UTC). Between surface (top of graph) and bottom (wide red line at lower part of graph) are two major layers of biomass. In the mid-part of the echogram is a deep scattering layer of mesopelagic fishes from 600 to 800 m. Above that is a layer of fishes migrating from about 500 m depth during day to the surface at night. This layer seems to include various components with different migration and distribution patterns, probably caused by the variety of species and sizes included in this layer. At surface during day there are layers of planktonic organisms. The deeper part of the echogram (greater than 900 m) had fewer fish echoes. The echogram patterns also demonstrate that topography affect density and distribution of marine organisms, particularly obvious where bottom peaks to 800 m depth. The three thin lines going from surface to deep water and back again like elongated Vs are recordings of instruments lowered from surface to about 1,000 m. The thick and short line at about 850 m at the first super station is a false-bottom echo.

is likely that depth and topography play major structuring roles, and along-ridge patterns appear more associated with water-mass distributions and circulation features than with other features, for example, fracture zones. This suggests that new studies, inevitably resource limited, would have to be truly depth stratified both in the pelagic and near-bottom zones and would further benefit from targeting features such as hydrographic frontal zones. Within this framework, an exploratory effort would perhaps benefit from a random stratified design. The strength of using multiple gears and instruments has been demonstrated and any departure from multidisciplinarity should be discouraged. Accommodating more elements such as all benthos components including meiofauna and microbes, and so forth, would be beneficial.

Expansion of exploratory programs into the South Atlantic has considerable interest because of its comparability with the North Atlantic MAR, and the level of knowledge of its fauna is very limited indeed. However, there may also be benefits from focusing on frontal zones and ridges that are suspected to be substantially different from the MAR. For example, the faster-spreading East Pacific Rise might be of special interest for comparison and contrasting with the MAR. Selecting study areas in varying pelagic productivity regimes would probably enhance knowledge even further.

6.5 Conclusions

The mid-ocean habitats associated with the MAR have high diversity and considerable, if presently undetermined, abundance of macro-and megafauna. The first observations of elevated richness and catches made by the *Michael Sars* expedition in 1910 were thus confirmed and considerably expanded by the multi-vessel operations conducted by MAR-ECO.

Primary questions addressed to what extent faunal components from eastern and/or western slopes contributed to the MAR fauna, whether there was a latitudinal change in the fauna, and to what extent this was affected by two main hydrographic features: the Sub-Polar Front and the Charlie Gibbs Fracture Zone (see, for example, Krauss 1986; Rossby 1999; Reverdin *et al.* 2003). A general pattern identified was that the MAR supports high biodiversity which is not fundamentally different in structure and composition from the adjacent continental slopes. Furthermore, the results do not indicate a high degree of endemism. In this the MAR does not appear as a chain of isolated seamounts. The patterns emerging from the benthic invertebrate data showed that the MAR constitutes an interface between eastern and western continental slope fauna, with a slight overweight of the former (Mironov *et al.* 2006).

The SPF seems to be a more important feature than the CGFZ in affecting the composition of the benthic invertebrate fauna (see, for example, Gebruk 2008a) and demersal fishes (King *et al.* 2006; Bergstad *et al.* 2008b). Similar conclusions were reached for zooplankton (Gaard *et al.* 2008; Hosia *et al.* 2008; Stemmann *et al.* 2008), although in zooplankton the SPF constitute more of a marked boundary for southern than northern species. Variation in the pelagic fauna is primarily related to depth, and the bathypelagic fish assemblages show a high degree of consistency from Iceland to the Azores (Sutton *et al.* 2008). Overall, the abundance of fishes declines with depth, but unexpectedly the pelagic fishes showed a biomass maximum in the bathypelagic zone between 1,500 and 2,300 m and in the benthic boundary layer, 0–200 m above the bottom regardless of depth.

For many taxa (see, for example, phytoplankton, crustacean mesozooplankton, pelagic decapods, bioluminescent organisms, mesopelagic acoustic scatterers, whales, and seabirds), there appeared to be a maximum along-ridge abundance in association with the SPF, but this frontal zone spans a considerable latitudinal range (48–53°N) and varies temporally in character and configuration. Whales appeared associated with areas of steeply sloping bottom.

Several species were rare, especially benthic invertebrates, and some were new to science (Fig. 6.8). Only

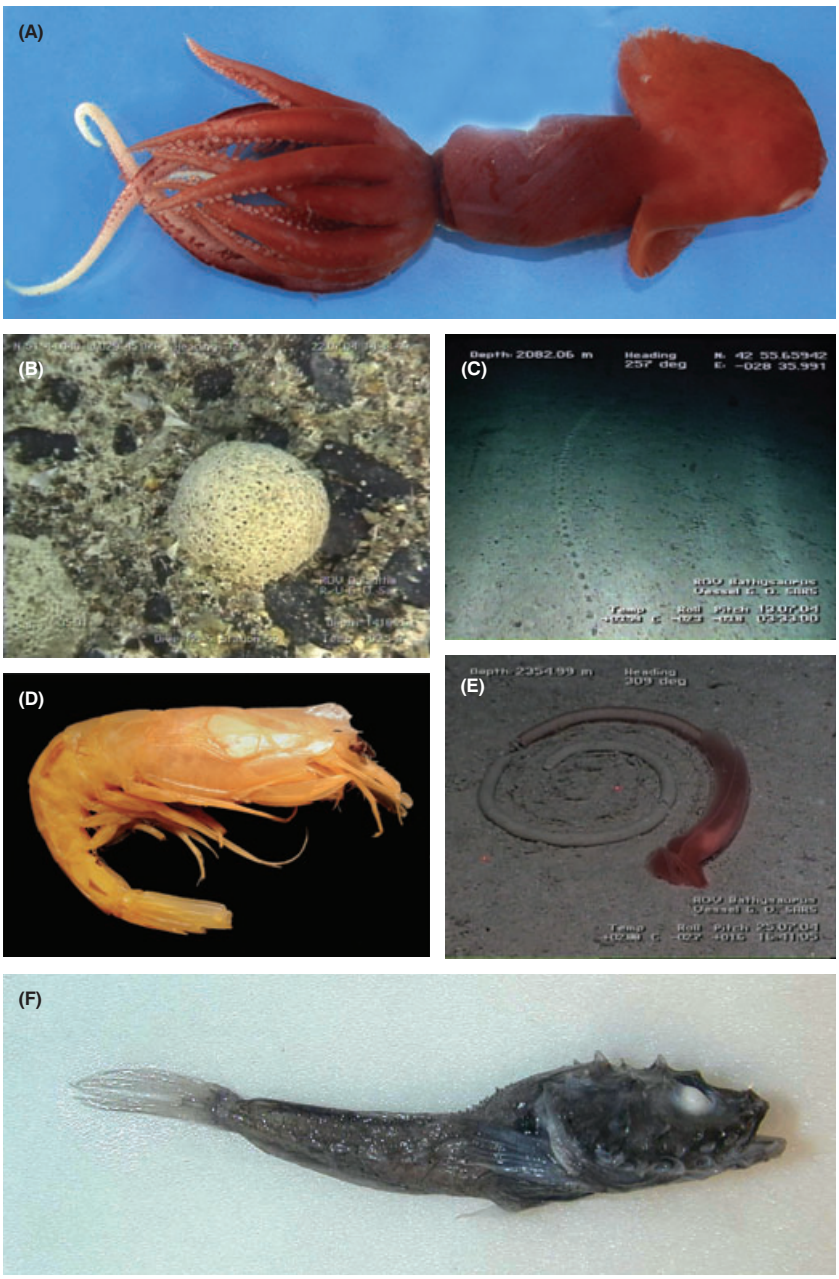

Fig. 6.8

Representative new species and remarkable observations. **(A)** Sloan squid, *Promachoteuthis sloani* Young *et al.* 2006; **(B)** giant protist family Syringamminidae; **(C)** mysterious track-like holes of unknown origin; **(D)** *Altelatipes falkenhaugae* Crosnier and Vereshchaka 2008 (© Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); **(E)** undescribed enteropneust; **(F)** *Cottunculus tubulosus*, Byrkjedal & Orlov 2007 (courtesy of Ingvar Byrkjedal).

extended sampling can tell whether these represent species endemic to the MAR. The rich collection of MAR animals, now archived at the Bergen Museum, will certainly be useful for taxonomic, phylogenetic, and other types of study for many decades.

Sampling extended to the adjacent abyssal plains would be necessary to determine to what extent ridge-associated abundances are especially high. Such sampling would be of particular interest to gain more insight into the midwater biomass maximum found over the ridge for pelagic fishes.

The MAR-ECO sampling only provided a "snapshot" impression of the faunal composition and distribution. With the exception of some acoustic landers deployed over a longer time span, the sampling did not cover circadian or circumannual time series. Thus, the results tell nothing about faunal responses to periods of plankton blooms, and nothing new can be said about possible temporal life-history phenomena such as vertical and horizontal migration, reproduction periods, and special reproduction areas. Diel migration patterns could even change over the annual cycle, and possible seasonal changes in the occurrence of the benthic boundary layer are still unstudied.

The benthic boundary layer community is very difficult to sample adequately with the gear that was available to MAR-ECO. The species composition of this assemblage is therefore not well known. Such a study might be suspected to yield more insight into the abundance of nekton in the benthic boundary layer. Furthermore, studies of meiofaunal and microbial communities and processes were not included in the MAR-ECO project.

Food web structures of the MAR communities have been determined for the first time based on studies combining analyses of stable isotope ratios, fatty acid profiles, and traditional determination of diets from identification of gut contents. Some insight has also been gained from studies of fish parasites (Klimpel *et al.* 2008). Some inferences on the top predator feeding ecology were made by comparing occurrences of predators and prey (Doksæter *et al.* 2008). Major issues for the future are the estimation of rates, selectivity studies in relation to prey fields, and the predation on and by gelatinous organisms. MAR-ECO did not collect data to assess the significance of microbial loop pathways. Seasonal feeding and growth studies, and perhaps *in situ* experiments to determine rates would provide substantial advances.

At the time of year studied (June–August), highest primary production was observed in the region south of the CGFZ. Characterized by a well-defined northern boundary and an extended mixed area extending southwards, the frontal area and the North Atlantic Current have a major influence over a large sector of the ridge. We hypothesize that differences in organic carbon export, prevailing bottom water temperature, and topography combine to determine benthic species composition.

Future work should be directed to determine surface production and pelagic to benthic fluxes over a wider latitudinal range than is currently being investigated. The physical interaction of the pelagic biota with the ridge needs to be examined at spatial scales from meters to the whole ridge system. Progress will depend on technological developments, notably fixed and mobile autonomous instruments, new tagging and tracking systems, and so forth, that can overcome the limitations of shipborne measurements.

A major challenge is the spatial and temporal scale of phenomena in the pelagic realm. The bio-physical environment on the MAR region is very complex, and only remote sensing methods provide the regional and temporal scales required to detect seasonal and inter-annual changes. Frequent cruises at different times of the year would be necessary to reach a full understanding of events and processes.

Acknowledgments

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